PSYCHOLOGICAL LITERATURE.

1.—NERVOUS SYSTEM.

Untersuchungen über die Physiologie der Froschhirns. DR. J. STEINER. Braunschweig, 1885.

Ueber das Centralnervensystem der grünen Eidechse nebst weiteren Untersuchungen über das des Haifisches. Prof. J. STEINER. Sitzungsberichte d. Königl. preusischen Academie d. Wissenschaften zu Berlin. XXXII. 1886.

Die Functionen des Centralnervensystems und ihre Phylogenese. Zweite Abtheilung; Die Fische. Prof. J. STEINER. Braunschweig, 1888.

The work of this author on the physiology of the central nervous systems of the fish, amphibia and reptiles, has already continued for nearly ten years. Since the first paper on the physiology of the frog's brain, his general plan has widened, so that in his last publication he states his problem as the study of the development of function in the brain and cord of the lower vertebrates. In this study he is guided by the same general rules that control morphologists in tracing the phylogeny of structure. This might be called a chapter in comparative physiology, but in that case it is only fair to add that it is undertaken from the standpoint of the doctrine of evolution, which certainly adds a fresh interest to the results. This is perhaps not quite so novel as Steiner feels it to be, but that is a small matter in comparison with his observations. The technique used was excellent, and all precaution was taken to escape confusing and doubtful results which should depend on careless operations. The most suitable places for work were chosen, and to that end the principal study of fishes was made at the Naples station, where the facilities were best. The results are stated for each group of experiments, and then in a separate section the theoretical considerations are dealt with alone. This theoretical portion is certainly of interest, but when, for instance, it takes the author into speculations on the origin of the forebrain of the vertebrates, he is perhaps carried too far. Taking the papers in chronological order, the physiology of the frog's brain comes first, and this order is the best to follow, as the physiology of the central nervous system in the frog is better known than that of the other animals employed.

Rana esculenta was used, and the cerebral hemispheres were first removed. Such a specimen remains quiet, as a rule, when not in the water. If excited by mechanical stimulation, makes one or more jumps, and then comes to rest. When jumping it can see, and so avoid objects in its path. When the path is free, locomotion is in a straight line, but if there is an obstacle in the way, it, under certain conditions, either jumps over or around it. Although, when quiet, threatening motions of the hand are disregarded, yet the same specimen, once started in a series of jumps, avoids capture, often with unexpected success. The conditions that determine whether the frog shall jump over an obstacle to be avoided, are that the obstacle be not too high, for if too high the frog will not even make the attempt; and that it shall cast a dark shadow in the path, for if a plate of clear glass be put in the way, the frog jumps *against* it. Where the object is too high, the frog avoids it by jumping to one side. Something of the direction of leap

in reference to an obstacle can be predicted from the motions of the frog's eyes. This same specimen balances well on a board, the plane of which is varied in the usual way. In many cases the frog slips when being thus tested, and to prevent injury the observations were made over water. When put in the water the frog swims to the edge of the aquarium, then stops swimming, and some specimens seek to get out of the water before they come completely to rest. This performance varies with different individuals, and with the same individuals at different times. It appears that when the air is warm, and the light bright, they are most likely to execute this final act. When put on its back, such a frog at once turns over to the normal position. In discussing these observations, Steiner points out that the loss of the hemispheres removes all spontaneity from the specimen. The so-called spontaneous movements on land are probably due to unobserved stimuli. Though nothing could appear more spontaneous than the swimming motions in the water, yet these are almost certainly due to the stimulus of that medium, for when the frog leaves the water the motions cease. Balancing and turning from the back to the normal position, Steiner argues to be dependent on the tension of the muscles connecting the trunk of the body with the head. We shall not enlarge on this point, on which he lays considerable stress, further than to state that he makes out a strong case. One experiment of interest in this connection is, that if the skin be removed from the back of such a frog and then he is laid on his back, he nevertheless turns over, showing that the action is due to something besides skin stimulation. In another connection Steiner brings out the fact that of the cerebral hemispheres it is the basal portion that is most important to the frog, for if the mantels of the hemispheres alone be removed, the specimen appears perfectly normal.

In the next operation the hemispheres plus the interbrain were removed. When this is done with a knife the optic nerves are also severed, and the frog is blind. This frog can jump fairly well, but does not pull himself together at the end of a leap with the same rapidity and sureness as one which has lost his hemispheres alone. He swims normally when put in the water, but does not try to climb to the edge of the tank. When laid on the back he will turn over; but when the experiment of balancing is tried, although the head is moved as the plane of the board is changed, no effort is made to get the body into a balanced position. Such specimens still croak reflexly. The interbrain is further a centre for the chromatophores in the skin. After operation all specimens become dark, and remain so persistently. To meet the objection that the loss of sight was responsible for some of these results, Steiner severed the thalamencephalon without cutting the optic nerves. Though such a frog can see, this advantage did not modify his action in any of the points just mentioned. To explain these results, Steiner assumes that the interbrain is a centre for sensations from the muscles, joints and skin, and that it is the loss of these sensations which causes the additional disturbance.

When the optic lobes, or mid-brain, as Steiner prefers to call them, are removed, a new complication appears. If the removal is not strictly symmetrical, forced movements occur. To this subject Steiner gives much attention, and such movements form an important criterion in his later speculations. In this connection, however, the cases where they do not occur will be specially considered. On mechanical stimulation, the frog without his mid-brain leaps normally. He is blind, and jumps against obstacles. When put in the water he swims, but in an uncoördinated manner. Considering the *lobi optici* as made up of a roof and base, for each lobus has a central cavity, it appears that the roof has no motor function, but is connected with vision alone, whereas the base has

motor functions. After the base is removed, the "croak" reflex cannot be obtained. Besides the loss of the special function of vision located in this region, there is the more general disturbance which might be considered as due to the removal of such central elements as were supposed for the interbrain.

When the cerebellum of the frog is removed, in addition to the parts lying cephalad of it, there is no additional disturbance. When, however, the cerebellum alone is removed, a slight trembling of the limbs, on certain occasions, and a loss of exactness in some of the muscular movements, were the symptoms observed.

Finally, if the most cephalic portion of the medulla oblongata is cut off, a marked change occurs. Though on mechanical stimulation the limbs are moved, there is no locomotion. The frog does not rest in the normal position, but flat on its belly; when placed on the back, it remains there. Put into water, no swimming motions are excited. In considering the remarkable effects which follow this last operation, Steiner reaches the conclusion that this region contains a coördinating centre for all the muscular motions, or a centre for locomotion. This centre is prominently brought out in the study of other forms, and to it therefore Steiner attaches great importance.

In those cases where the brain, including the mid-brain *(lobi optici)*, had been removed, certain irregularities of reaction were observed, which led to a further study of the region. This was made by first removing the cephalic third of the mid-brain. Such a frog was but little different from one which had lost the interbrain alone. He still gave the "reflex croak." When the cephalic two-thirds were cut away, stimulation did not make him creep or jump, but the frog moved backwards. This backward motion was then a function of the caudal third of the mid-brain. By the removal of parts of the brain in an asymmetrical manner, a great variety of forced movements can be produced. A review of these, while of much interest, must be omitted here.

Having thus given in some detail the observations on the frog, those on the other animals may be stated more briefly. When the forebrain of the green lizard *(Lacerta viridis)* is removed, the animal remains motionless as if asleep, from time to time opening its eyes. When irritated it wakes up, so to speak, runs off a short distance, and again relapses into its dormant state. In this case locomotion is normal, but the lizard runs as readily towards the operator as away from him. It has no fear. It can at the same time see, for it avoids obstacles in its path. The lost functions are located, however, in some portion of the hemispheres which is not the mantel, for when that only is removed the creature runs when frightened by a movement towards it, and eats and drinks voluntarily. The removal of the interbrain plus the hemispheres introduces chiefly a change in locomotion, whereby the specimen when excited runs a few steps and then gives a jump, as the normal animal does when jumping from a wall.

Making, again, a distinction between the roof and basis of the mid-brain, removal of the roof is without effect on the locomotion. At the same time the animal can still *see*, though it appears amblyopic. Removal of the entire mid-brain does not interfere with locomotion. If the caudal portion is left in place, the tendency to motion backwards comes out far more strongly than in the frog. The removal of the cerebellum appears to be without any special effect. Finally, the removal of the anterior portion of the medulla oblongata abolishes locomotion, so that we have in this region, as in the frog, a coördinating centre of prime importance. If a specimen in this last condition have its cord severed at short intervals with scissors, it is found that when a region near the middle of the trunk is reached, the tail and posterior extremities commence what are apparently spontaneous and regular movements, which are

clearly locomotory. It would appear then that there are, in this portion of the cord, centres which were comparable to the more important centres in the medulla oblongata. In the discussion of fish, this point is brought out more clearly.

Steiner opens his study of fishes by some tests on the function of the fins and tail. The tail is preëminently the organ of locomotion, whereas the fins are used to keep the animal at a given level in the water, to steer, to stop and to move backwards; with maintenance of equilibrium they have nothing to do. *Squalius cephalus* (v. Siebold) was the fish used for these experiments. In removing different parts of the brain, the improvements in technique employed were artificial respiration, to keep the fish quiet during the operation, and a useful method of closing the wound by a gellatine cap, so that healing is facilitated and water prevented from entering the cavity of the skull. The removal of the forebrain from this bony fish (*Squalius*) is followed by no loss in locomotion. Further, the movements of the specimens are not to be distinguished from the normal, and are voluntary. When food is put in the tank it is seized by such a fish with unhesitating exactness, and a worm is distinguished from a piece of string before it is taken. Fish thus operated play together. We have here the very remarkable case of the seat of voluntary activity elsewhere than in the forebrain. Steiner argues that the forebrain once possessed these functions, but becoming degenerate (as it certainly is), parted with them to the more caudal divisions. In this fish an interbrain is not available for separate study.

As in other cases, stimulation of the roof of the mid-brain causes movements of the eyes, whereas the removal of the roof renders the fish blind. In this case the removal of the entire mid-brain has a very marked effect. Regular breathing continues, but no voluntary locomotion occurs, and equilibrium is affected. When the fish is mechanically stimulated, however, it makes locomotory movements. The cerebellum, which has really an enormous development in these fish, may be removed without causing any disturbance in the locomotion or equilibrium of the specimen. The cephalic portion of the medulla in *Squalius* possesses elevations not found in the medulla of the frog, for example. When this region in *Squalius* is removed, breathing ceases, and the animal is dead. This complication is avoided, however, when an eel is used. In this fish a section here abolishes locomotion, but leaves the breathing intact. If these observations are to be harmonized with those on the frog, the locomotor centre must be considered as somewhat variable in position, for in the fish the removal of the mid-brain produces much the same result as did removal of the cephalic portion of the medulla oblongata in the frog.

Steiner next gives his attention to *Amphioxus lanceolatus*, and by way of preface describes this creature in the normal condition as swimming only so long as is needful to hide itself in the sand, and then remaining there till it is again disturbed. Of course, where locomotion is thus reduced in the normal creature, it could not be expected that much variation could be experimentally effected. If a specimen is cut in half in the middle, the two parts, when irritated, swim independently, cephalic end first, and preserve their equilibrium. A single specimen may be cut in three or four pieces, and each piece swims alone. If the parts show signs of exhaustion, simply putting them in a bath of picro-sulphuric acid, of at least one per cent., stimulates them to remarkable activity. Steiner concludes that the body of *Amphioxus* consists of a series of equivalent metameres, each of which has its own centre for locomotion, and that there is no principle centre as in the other forms thus far studied.

The shark was next examined, the dog-fish (*Scillium canicula*) being

chiefly used. When the fore-brain was removed, and the specimen replaced in the tank, it swam about for a time, showing that locomotion was undisturbed, and then sank to the bottom, where it remained quiet for an indefinite period. The test was made to see if such a shark would feed. Though the test was continued for two months, the specimen still refused to take food. In some specimens the olfactory bulbs alone were separated, and in these the result was the same as that which followed the removal of the hemispheres. Removal of the olfactory bulb on one side only, did not interfere with the spontaneous taking of food. When the inter-brain as well as the hemispheres are removed, the *nervi optici* are cut in the operation, and the animal becomes blind, but there appears no other additional disturbance, save that the specimen tends to come to rest in a corner of the tank a trifle sooner than one which has lost merely the fore-brain. As usual, there is no observable disturbance after removal of the cerebellum, though it is rather bulky in these fish. The roof of the mid-brain is found to be a visual centre, for when removed the sharks became blind. With removal of the base of the mid-brain spontaneous locomotion is abolished, but the power remains, as appears on mechanical stimulation. There is an increased difficulty in maintaining equilibrium, despite vigorous efforts to do so. In the cephalic portion of the *medulla oblongata* is a locomotory centre; for when the brain, including this region, is removed, the power of locomotion is lost, even in response to mechanical stimulation. Continuing the observations of the spinal cord, some very remarkable results were obtained. The headless body of the shark will swim the entire length of the long aquarium, stopped only by the side wall; then, when turned about, will swim back to the place from whence it started. The relations in this case suggest that in the medulla there is some portion which acts to inhibit the spinal cord, for when this is removed the cord exhibits much greater activity. Steiner, however, takes the view that, since the cord is subordinated to the brain, that fact in the first place is additional proof of the location of a general centre for locomotion in the cephalic portion of the oblongata; and further that, since the cord is controlled, even in so slight a degree, by mere cephalic centres, it is condemned in the higher forms to lose its independence. In this connection, the spinal cord in the Rays was tested, *Torpedo oculata* being used, and it was found that, while the fish possessing only the spinal cord remained quiet when put in the water, it swam on stimulation, showing that the cord in this case, too, is possessed of locomobility, (Steiner's word, *Locomobilität*, meaning capability of locomotion).

Among the Ganoids the Sturgeon (*Acipenser sturio*) was found possessed of cord locomobility similar to that of the shark. Curious is the reaction of the lampreys. *Ammocœtes*, and the two forms of *Petromyzon*, were all observed. If one of these is cut in two in the middle, the head end makes regular swimming motions in the water, and the tail end remains quiet. When, however, the motionless part is put in the bath of picric acid, previously described, it swims in a most satisfactory manner. From this Steiner concludes that in the head end of the lampreys, there is a general centre for locomotion, and that similar centres exist in the cord also, but in this latter situation are so reduced in irritability that only some strong stimulus can bring them into action. This apparent loss of function in these cases where the function is, however, shown to be present, by the use of special stimuli is a suggestive observation. The spinal cord of the eel is excitable in picric acid, but in this animal the swimming motions are made with the caudal end of the body only, showing, as it appears, a localization of the mechanisms in that portion of the cord.

Taking up next the forced movements in bony fish, it is observed that removal of one cerebral hemisphere, or of one half the cerebellum, is

without effect, whereas removal of half the mid-brain causes circus movements towards the sound side; and a cut through one half of the medulla, rolling movements towards the operated side. In this connection some observations on the flat fishes (*Pleuronectidæ*) were made, *Solea vulgaris* being the species employed. Steiner argued that if the circus movements in the normal fish were made in the horizontal plane, and if the flat fish represented a form in which the body of the fish had rotated ninety degrees about its long axis, that if forced circus movements were established in a flat fish by operations on the brain, then the circus movements would take place in a vertical plane. Experiments showed this to be the case in a very exact way. In the sharks the result of asymmetrical removal of parts of the brain has the same consequences as in the bony fish, with the exception that injury to the interbrain, which cannot be sectioned independently in the bony fish, produces in the sharks temporary circus movements. A lesion on one side of the spinal cord would not be expected to produce forced movements; nor does it do so. Steiner concludes, therefore, that forced movements are a function of the general motor center, and such being the case, the movements themselves can be used to determine the existence of such a motor center. The next following observations are the most novel and striking which the author has obtained, and if confirmed will be an important step in our knowledge of the nervous system. If a shark which has been so operated as to perform circus movements is beheaded, the headless trunk continues to perform the same circus movements. In the case of rolling movements, beheading puts an end to them. The trunk, however, does not acquire this capability to perform independent circus movements unless at least ten hours have elapsed between the original operation and decapitation. Apropos of these observations, Steiner has something to say of memory as a function of living matter, and some criticism of apparently similar results obtained by other authors, but nothing more definite by way of explanation.

The record of experiments ends here, but there are some general conclusions and reflections on the significance of the fishes' brain. It is here that Steiner argues that, because in the shark voluntary activity is strictly bound down to the olfactory lobes, that therefore the forebrain of the vertebrates has developed phylogenetically from an olfactory centre, a conclusion that seems somewhat hasty. In discussing the genealogy of fishes from the data thus collected, Steiner takes occasion to define the brain as a general motor centre, in connection with at least one of the special senses. The spinal cord, under the control of one coördinating centre, is by Steiner developed from some ideal form composed of a series of equivalent metameres, each possessing locomobility to the same degree. When centralization of this function occurs, it takes place at the head end of the animal, but the order in which the function is lost in the spinal cord is such that it first disappears in the most cephalic portions of the cord, while it remains longest in the most caudal portion—a conclusion which has some indirect support from other sources.

Strictly considered, investigations in the functions of the semicircular canals do not follow here, but in an appendix Steiner has some interesting observations on these organs in the shark, which may thus be summarized: In *Scyllium canicula* and *Catalus*, the cartilaginous canals were opened, and the membraneous portions removed, together with their ampullæ. Whether this was done on both sides or on one side only, the result was the same, *i. e.*, locomotion remained perfectly normal in all cases; no disturbance of equilibrium. When, on the other hand, the vestibulum is opened, and the otoliths either removed or only disturbed, locomotion becomes abnormal, the disturbance consist-

ing usually of rolling movements towards the operated side. The results in all cases are without exception. Further, removal of the semicircular canals, and filling the vestibulum with melted paraffin, cause no disturbance of locomotion or equilibrium. Since neither removal of the semicircular canals nor complete exclusion of the vestibulum, closing it with paraffin, cause any disturbance, but only mechanical stimulation of the latter gives rise to the rotatory movements, Steiner attempts to explain the disturbance as due to direct lesion of the cephalic end of the medulla oblongata, at the point of emergence of the auditory nerves. This view is very hypothetical, and the conclusion that the condition of things in the shark holds for the higher vertebrates, also has too slender a foundation to be valuable.

This lengthy notice does not touch on many smaller observations which the author has recorded, nor does it point out what is new and what old in the observations cited. So important, however, is the fundamental idea that development of function is as real a thing as development of form, and so often is the idea disregarded in biological speculation, that it has appeared worth while to give a full statement of this work of Steiner, which so well illustrates the possibilities of this line of investigation.

Histologische Studien an der menschlichen Netzhaut. PROF. KUHNT in Jena. Jenaische Zeitschrift für Naturwissenschaft, xxiv, 1. p. 177.

The investigation of Prof. Kuhnt (of which this is a preliminary notice) had two objects,—first, to determine what ones of the histological constituents belong to the tissues of support and connection, and what to the nervous elements; and second, to trace the connections of the nervous elements from the layer of fibres through to the rods and cones. He finds, contrary to the opinion of Borysiekiewicz, that the radial fibres have one nucleus only, and that the internal limiting membrane belongs to the vitreous body. He has no theory to offer as to the function of the reticular layers, but thinks that they cannot play the part of insulators, because for this purpose they would be most needed in the fovea, where they are thinnest. [May they not act as veils, to diminish the amount of light which reaches the rods and cones, and so to facilitate the concentration of the attention upon the sensations of the fovea?] In regard to the nervous parts of the retina, he was so successful as to obtain, after many failures, three good preparations showing a plain connection between ganglia of the optic nerve (ganglionic layer) and of the retina (inner nuclear layer),—which has not been accomplished before. The connecting fibre sprang, in each case, from the body of the ganglion, and not from any of the large processes, and it had only inconsiderable varicosities. Of the fibres which come from a cell of the inner nuclear layer, it is the middle one of an umbel of fibres which joins onto a cell of the outer nuclear layer. It was determined from a large number of observations, that every ganglion of the outer nuclear layer is connected with a single cone, and with a larger or smaller number of rods, according to its more peripheral or more central position in the retina. Less frequently, it was made out that a single pigment cell encloses the cone and the group of rods which communicate with a single nuclear cell. [That an arrangement of this sort must prevail, had been affirmed before by Emil duBois-Reymond, from a consideration of the numerical relations of the fibres and of the rods and cones. A cone, with a group of rods around it, all attached to one ganglion of the outer layer, ought henceforth to be called a *cone-system.*] Under the action of a given coloring reagent, not only did the color of the processes of the ganglia vary with their thickness and with their distance from the cell, but the ganglia themselves were sometimes colored throughout, sometimes only near the nucleus, only in the